

PRE-1941 EGG SHELL CHARACTERISTICS OF SOME BIRDS¹

D. R. OSBORNE AND R. WINTERS, Department of Zoology, Miami University, Oxford, Ohio 45056; 127 Balyeat Ave., Van Wert, Ohio 45891

Abstract. Parameters and techniques used to characterize avian eggshells are reviewed. Elongation, volume and thickness indices were calculated to estimate the shape and size of 1145 eggs (328 sets) representing 18 orders, 54 families and 253 species of the Clark K. Lloyd Collection at Miami U., Oxford, Ohio. The study includes eggs of species from 13 countries and 37 states collected prior to the widespread use of pesticides. Fifty four species came from Ohio and 43 from California. Sixteen species are considered rare or endangered, or have declining populations. A comparison of egg volumes as determined by Paganelli *et al* (1974) was made and differences ranged from 0.7% to 22%.

OHIO J. SCI. 77(1): 10, 1977

During the last quarter of the 19th and early portion of the 20th century many oologists attempted to build up comprehensive collections under regulations set forth by national and international societies. These collections are presently housed in museums and undoubtedly some are still in private collections. At the request of the American Ornithologist's Union's Committee on Research, a project was initiated in 1966 to survey egg and bird collections in the United States and Canada. Of the 160 egg collections found, five are housed in Ohio museums (Banks *et al*, 1973; Clench *et al*, 1976). Most collections consist of full clutches (sets) along with date and location collected and are important resources for determining variability within clutches as well as intraspecific relationships. Changes in eggshell characteristics can also be related to geographic location and to different aspects of breeding biology before and after the widespread use of persistent pesticides.

The present paper reviews the various parameters and techniques used in studies on eggshells, and documents eggshell characteristics of 1145 eggs from the Clark K. Lloyd collection, presently housed at Miami University, Oxford, Ohio. The history of the collection has been described by Hefner (1974). The

collection contains 328 egg sets from 18 orders, 54 families and 253 species, mostly from North America, which were obtained between 1887 and 1940 (table 1). It includes eggs of species from 13 countries and 37 states. Most species are represented by only one clutch of eggs. The collection is important because it was accumulated prior to the widespread use of pesticides and because it contains a large sample collected from a localized area in the interior of North America. Fifty four species (57 sets) are from Ohio; with 50 from Butler County. Because of the limited area of the collection the data should not be considered as a representative cross-section of Ohio birdlife.

METHODS

Traditionally figures in texts report the size of egg by average value of length and breadth (e.g. French, 1973), and sometimes range value (e.g. Bent, 1919). Recent texts such as the *Handbook of North American Birds* (Palmer, 1962) have included measurements of the curvature of the two ends of the egg. This more accurately specifies the shape of the egg, independent of its size. The rationale for these measurements is discussed by Preston (1968).

We reported standard measurements of length, breadth and weight because they are easily obtainable in the field and laboratory. These values were then used to calculate the eggshell indices of elongation, volume, and thickness (table 1). Greatest length and breadth were measured with a vernier caliper to the nearest 0.1 mm and weight to the nearest 0.1 mg. Species and scientific names are

¹Manuscript received March 25, 1976, and in revised form August 9, 1976 (#76-31).

listed and arranged according to the AOU 1957 check-list.

EGGSHELL PARAMETERS

Shape Index. Eggs of various species differ considerably in shape, ranging from the near spherical eggs of the Hooded Merganser (*Lophodytes cucullatus*) to the conical eggs of the Golden Plover (*Pluvialis dominica*). Several different indices have been used to approximate shape. Most involve the dimensions of length and breadth. The shape index, $B/L \times 100$, developed by Romanoff and Romanoff (1949), has been used in the studies on egg characteristics in House Wrens, *Troglodytes aedon*, (Kendeigh *et al*, 1956) and Shags, *Phalacrocorax aristotelis*, (Coulson *et al*, 1969). A low index indicates a relatively long and narrow egg; a high index a short and broad egg.

Recently, Preston (1968) derived mathematical formulae to quantify the amount of curvature of the two ends of eggs in terms of asymmetry and bicone. These measurements can be made with a profile-copying machine (Preston, 1953) or a modified spherometer (Gemperle and Preston, 1955; Preston, 1957). In addition, Preston (1968) used the length divided by the breadth (L/B) as a measure of *elongation* (K of Schönwetter, 1960-72), and argues that this plus the values of asymmetry and bicone define egg shape and size with virtual completeness. We have used Preston's (1968) *elongation* as an index of shape, recognizing its limitations, and have omitted asymmetry and bicone since the instruments required for these measurements were not available. Elongation is high for long narrow eggs and low for short broad eggs. Preston (1969) summarizes elongations of eggs from 63 North American families.

Volume and Volume Index. An estimate of volume was computed by the equation of Kendeigh, *et al* (1956):

$$V = \frac{\pi}{6} LB^2$$

where V , the volume, is mm^3 , L maximum length, and B maximum breadth in mm. The coefficient $\pi/6$ is approximately 0.524 and holds for eggs which are true

prolate ellipsoids. A coefficient of 0.51 was used to allow for the imperfect ellipsoid form of a number of seabird eggs (Stonehouse, 1966; Coulson *et al*, 1969). The coefficient is not suited for hummingbirds which lay blunt-ended eggs nor for grebes and tinamous which lay eggs pointed at both ends (Preston, 1974, Tatum 1975).

Actual measurements of internal volumes are more accurate than external volumes calculated from egg dimensions, but such measurements are not always practical for eggshells, and indices must suffice. Worth (1940) found for eggs of domestic fowl (*Gallus gallus*) that volumes obtained by water displacement were 15% less than those calculated by the ellipsoid formula. Coulson estimates the internal volume from external measurements to average about $0.487 LB^2$, about 9.3% less than the ellipsoidal formula would give. Of this, 3% is due to bicone and about 6% to shell thickness (Preston, 1974).

Equations have been developed relating surface area to fresh egg weight and shell volume (Paganelli *et al*, 1974; Shott and Preston, 1975). Although error ranges only from 1-3%, most of these equations are not applicable to eggs whose contents have been blown. Egg volumes have been shown to vary according to the sequence of laying (Kendeigh *et al*, 1956) and season (Coulson *et al*, 1969), and have been useful in estimating the age composition of populations (Coulson *et al*, 1969).

Thickness and Thickness Index. Thickness of whole eggshells can be measured with a modified Starett 1010M dial micrometer having a curved rod which is inserted through the blow-hole (Anderson and Hickey, 1970a). Measurements by this method would also include the firmly attached membranes. The main disadvantage of this technique is that it can only be used on large eggs with large blow-holes.

Another method is a Vicker's Image Splitter attached to a microscope (Alsop, 1972). With this technique measurements can be made in microns regardless of the size of the blow-hole. Microscopic observation enables shell membranes to be visually separated from the

eggshell itself and not be included in the thickness dimension.

Shell thickness is directly related to egg volume (Olsson, 1936) and many species which lay small eggs have relatively less shell and thinner shells than larger eggs of other species (Grossfeld, 1938; Asmundson *et al.*, 1943; Romanoff and Romanoff, 1949). Shell thickness is also related to total egg weight. Ar *et al.*, (1974) calculated the change in eggshell thickness with egg weight from data of Schönwetter (1960-72), which then were used to predict total functional pore area in 29 species of birds. Thickness of eggshells was found to be proportional to the 0.456 power of fresh egg weight but this is not applicable to eggshells void of their contents.

Thickness index is defined as the weight (mg) of the shell divided by the product of length and breadth in mm (Ratcliffe, 1967; 1970). We used Ratcliffe's index of thickness because of its reliability (Anderson and Hickey, 1970b; Burger, 1973). Thickness and thickness index have recently been useful in documenting the relationship between eggshell thinning and the increase of chlorinated hydrocarbons in ecosystems, particularly in raptorial and fish-eating birds (c.f. Hickey and Anderson, 1968; Anderson *et al.*, 1970; Porter and Wiemeyer, 1969), and more recently in passerines (Alsop, 1972). The only record we know of where eggshells become thicker shelled (but smaller) is that of Jefferies (1969) for the Bengalese Finch (*Lonchuer striata*) exposed to chlorinated hydrocarbons.

Sample Size. Finally, it is necessary to decide how many eggs need to be sampled for confidence in our "means" or averages. Preston (1968) selected a standard error of the mean of 0.7% as being acceptable and concludes that 20 eggs, one per clutch (i.e. from different parents), constitute an adequate sample. This sample size was used for most birds listed in the *Handbook of North American Birds* and involved visits to 20 different museums and private collections. The question of using whole clutches or one egg per clutch in studies of eggshell thickness was rigorously tested by Klaas *et al.*, (1974). They found that differences among measurements of the

same eggs contributed little to the sample variance, whereas differences among eggs within clutches contributed nearly as much as differences among clutches. They concluded that it is more efficient and less costly to collect entire clutches, and estimated 8-11 clutches were adequate for detecting differences of 10% in shell thickness.

RESULTS

Elongation, volume and thickness indices were calculated for 1145 eggs (328 sets) representing 18 orders, 54 families and 253 species of birds (table 1). Thirteen countries and 37 states are represented. The largest sample comes from Ohio (54 species) followed by California (43 species). Because of the small sample size (most species are represented by only one clutch) species common to two localities were not compared statistically for geographic differences. Egg parameters are also included for 16 species considered rare or endangered, or which have undergone recent population declines (Wallace *et al.*, 1972; Smith *et al.*, 1973).

Average elongation for the class Aves is 1.36 (1.13-1.75) which is similar to the class average of 1.39 (1.19-1.75) found by Preston (1969) for representatives of 63 North American families. Owls of the family Strigidae have the most spherical eggs (1.16; 1.13-1.20) and the Murres of the family Alcidae the most elongated (1.71; 1.67-1.75). Families averaging elongations of 1.60 or more are anhingas (1.60), gannets (1.61), cormorants (1.64), and loons (1.65). Families with low elongations are Sittidae (1.22), Accipitridae (1.24), Phasianidae (1.24) and Parulidae (1.29). Our family averages were within 0.03 units of averages found by Preston (1969). New families not previously recorded include Apodidae (1.54) and Sittidae (1.22).

Egg volumes ranged from 0.45 cm³ for the Black-chinned Hummingbird to 223 cm³ for the Sandhill Crane (table 1). In general larger birds lay larger eggs. Based on total egg weight, Paganelli *et al.*, (1974) calculated egg volumes for 29 species of birds, 14 of which are represented in our study. A comparison of egg volumes as determined by the formulas of Kendeigh

TABLE 1
Average Eggshell Characteristics of Bird Eggs Collected Prior to 1941

Species†	No. eggs‡		L(mm)		B(mm)		Wt(gm)		L/B"		Vol. (cm³)#		Thickness§	
	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH
Common Loon (UNK) <i>Gavia immer</i>	1	—	89.2	—	54.2	—	14.2	—	1.64	—	137.31	—	2.94	—
Arctic Loon (NOR) <i>Gavia arctica</i>	2	—	88.2	—	52.6	—	11.1	—	1.67	—	128.21	—	1.97	—
Red-throated Loon (TX) <i>Gavia stellata</i>	2	—	72.5	—	44.5	—	6.3	—	1.63	—	75.45	—	1.94	—
Horned Grebe (CAN) <i>Podiceps auritus</i>	4	—	44.7	—	31.1	—	1.8	—	1.43	—	22.60	—	1.31	—
Eared Grebe (ND) <i>Podiceps caspicus</i>	10	—	43.2	—	29.2	—	1.7	—	1.48	—	19.31	—	1.32	—
Western Grebe (ND) <i>Aechmophorus occidentalis</i>	5	—	59.9	—	39.4	—	5.0	—	1.52	—	48.82	—	2.12	—
Pied-billed Grebe (MI) <i>Podilymbus podiceps</i>	8	—	43.4	—	30.2	—	2.0	—	1.44	—	20.74	—	1.46	—
Fulmar (SCOT) <i>Fulmarus glacialis</i>	1	—	70.3	—	51.4	—	9.3	—	1.37	—	97.32	—	2.58	—
White Pelican (TX) <i>Pelecanus erythrorhynchos</i>	3	—	88.3	—	56.3	—	16.7	—	1.57	—	147.22	—	3.36	—
*Brown Pelican (LA) <i>Pelecanus occidentalis</i>	3	—	71.5	—	50.2	—	9.2	—	1.42	—	94.26	—	2.56	—
Gannet (CAN) <i>Morus bassanus</i>	1	—	79.6	—	49.5	—	11.1	—	1.61	—	102.20	—	2.42	—
Double-crested Cormorant (MN) <i>Phalacrocorax auritus</i>	3	—	62.1	—	37.8	—	5.1	—	1.64	—	46.43	—	2.19	—
Anhinga (MS) <i>Anhinga anhinga</i>	5	—	55.0	—	34.4	—	2.7	—	1.60	—	34.11	—	1.42	—
Great Blue Heron (CA, NJ) <i>Ardea herodias</i>	10(3)	—	64.7	—	45.9	—	6.3	—	1.41	—	71.53	—	2.12	—
Green Heron (CA, FL) <i>Butorides virescens</i>	3(2)	4	40.7	38.6	29.0	28.9	1.1	1.1	1.40	1.33	17.90	16.90	0.94	0.96
Little Blue Heron (FL) <i>Florida caerules</i>	5	—	44.7	—	33.3	—	1.7	—	1.34	—	26.05	—	1.17	—
Reddish Egret (TX) <i>Dichromanassa rufescens</i>	3	—	50.8	—	35.8	—	2.5	—	1.42	—	34.07	—	1.35	—
Common Egret (MS) <i>Casmerodius albus</i>	4	—	57.1	—	39.3	—	3.4	—	1.45	—	46.25	—	1.53	—
Snowy Egret (FL) <i>Leucophox thula</i>	4	—	43.8	—	33.3	—	1.6	—	1.31	—	25.52	—	1.10	—
Louisiana Heron (TX) <i>Hydranassa tricolor</i>	5	—	43.7	—	32.4	—	1.6	—	1.35	—	24.02	—	1.18	—
Black-cr. Night Heron (UNK, NJ) <i>Nyctanassa nycticorax</i>	4(2)	—	51.9	—	36.8	—	3.0	—	1.42	—	36.71	—	1.58	—
Yellow-cr. Night Heron (TX) <i>Nyctanassa violacea</i>	4	—	50.2	—	37.3	—	2.6	—	1.34	—	36.59	—	1.37	—
Least Bittern (SD) <i>Ixobrychus exilis</i>	4	—	32.1	—	24.6	—	0.5	—	1.31	—	10.16	—	0.69	—
American Bittern (NY) <i>Bolaurus lentiginosus</i>	2	—	53.6	—	36.4	—	2.3	—	1.47	—	37.35	—	1.19	—
White-faced Ibis (UNK, TX) <i>Plegadis chihi</i>	5(2)	—	49.1	—	35.9	—	2.5	—	1.37	—	33.15	—	1.45	—
White Ibis (FL) <i>Eudocimus albus</i>	4	—	58.3	—	37.9	—	3.8	—	1.54	—	44.05	—	1.70	—

†Location collected other than in Ohio is in parenthesis. UNK=unknown, all other abbreviations of country, state, etc. as listed in the North American Bird Banding Manual, Vol. 1, 1976. Standard deviations were calculated but are not included in the table due to the small sample size in most cases.

‡Number of clutches other than one is in parenthesis.

"Elongation; length (L) in mm divided by breadth (B) in mm, after Preston (1968).

#Volume Index, after Kendeigh *et al.*, (1956).

§Thickness Index, after Ratcliffe (1967).

*Species considered rare or endangered, peripheral, or with recent population declines, after Wallace *et al.*, (1972), Smith *et al.*, (1973).

Species†	No. eggs‡		L(mm)		B(mm)		Wt(gm)		L/B"		Vol. (cm³)#		Thickness§		
	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	
American Coot (CA) <i>Fulica americana</i>	7	—	48.4	—	33.0	—	2.6	—	1.47	—	27.65	—	1.61	—	
Oystercatcher (DEN) <i>Haematopus ostralegus</i>	2	—	59.3	—	40.3	—	3.5	—	1.38	—	47.91	—	2.51	—	
Lapwing (ENG) <i>Vanellus vanellus</i>	3	—	44.6	—	32.3	—	1.4	—	1.38	—	24.31	—	0.98	—	
Semipalmated Plover (LAB) <i>Charadrius semipalmatus</i>	3	—	34.2	—	24.2	—	0.6	—	1.41	—	10.54	—	0.75	—	
Piping Plover (NY) <i>Charadrius melodus</i>	3	—	31.6	—	24.5	—	0.4	—	1.29	—	9.97	—	0.57	—	
Snowy Plover (CA) <i>Charadrius alexandrinus</i>	2	—	31.1	—	22.6	—	0.5	—	1.38	—	8.32	—	0.67	—	
Wilson's Plover (SC) <i>Charadrius wilsonia</i>	3	—	38.0	—	26.0	—	0.8	—	1.46	—	13.48	—	0.83	—	
Killdeer <i>Charadrius vociferus</i>	—	3	—	38.4	—	26.7	—	0.9	—	1.44	—	14.30	—	0.82	—
American Woodcock (NY) <i>Philohela minor</i>	4	—	39.0	—	29.1	—	0.8	—	1.34	—	17.32	—	0.75	—	
Common Snipe (CAN) <i>Capella gallinago</i>	3	—	39.3	—	27.3	—	0.8	—	1.44	—	15.30	—	0.73	—	
Long-billed Curlew (UNK) <i>Numenius americanus</i>	4	—	69.6	—	49.5	—	4.9	—	1.41	—	89.32	—	1.41	—	
Upland Sandpiper (NE) <i>Bartramia longicauda</i>	4	—	47.0	—	34.6	—	1.6	—	1.35	—	29.56	—	0.96	—	
Spotted Sandpiper (UNK) <i>Actitis macularia</i>	3	—	32.4	—	23.0	—	0.5	—	1.41	—	8.96	—	0.65	—	
Willet (TX) <i>Catoptrophorus semipalmatus</i>	3	—	54.1	—	37.5	—	2.4	—	1.44	—	39.98	—	1.21	—	
American Avocet (UT) <i>Recurvirostra americana</i>	4	—	52.6	—	35.0	—	2.2	—	1.50	—	33.77	—	1.17	—	
Black-necked Stilt (CA) <i>Himantopus mexicanus</i>	4	—	41.6	—	31.3	—	1.4	—	1.42	—	23.00	—	1.00	—	
Wilson's Phalarope (WY) <i>Steganopus tricolor</i>	3	—	32.3	—	24.1	—	0.6	—	1.34	—	9.87	—	0.72	—	
Northern Phalarope (ICE) <i>Lobipes lobatus</i>	4	—	29.9	—	21.0	—	0.3	—	1.42	—	6.93	—	0.54	—	
Glaucous Gull (AL) <i>Larus hyperboreus</i>	3	—	71.5	—	50.6	—	6.4	—	1.41	—	95.96	—	1.77	—	
Great Black-b. Gull (WAL) <i>Larus marinus</i>	3	—	76.7	—	53.5	—	5.2	—	1.43	—	115.58	—	1.27	—	
Western Gull (CAN) <i>Larus occidentalis</i>	2	—	73.7	—	49.7	—	6.9	—	1.49	—	95.47	—	1.88	—	
Herring Gull (CAN) <i>Larus argentatus</i>	2	—	73.0	—	51.6	—	6.8	—	1.41	—	102.13	—	1.80	—	
California Gull (UT) <i>Larus californicus</i>	4	—	63.9	—	45.5	—	4.7	—	1.40	—	69.55	—	1.62	—	
Ring-billed Gull (ND) <i>Larus delawarensis</i>	3	—	61.2	—	42.5	—	3.9	—	1.44	—	58.04	—	1.49	—	
Laughing Gull (VA) <i>Larus atricilla</i>	3	—	53.8	—	41.1	—	3.1	—	1.31	—	47.52	—	1.39	—	
Franklin's Gull (CAN) <i>Larus pipixean</i>	3	—	50.7	—	36.5	—	2.0	—	1.39	—	35.35	—	1.08	—	
Black-l. Kittiwake (ICE) <i>Rissa tridactyla</i>	2	—	55.6	—	40.5	—	2.5	—	1.37	—	47.91	—	1.13	—	
Forster's Tern (VA) <i>Sterna forsteri</i>	3	—	42.0	—	29.9	—	1.1	—	1.40	—	19.70	—	0.88	—	
Common Turn (VA) <i>Sterna hirundo</i>	2	—	44.1	—	30.7	—	1.2	—	1.44	—	21.78	—	0.87	—	
Arctic Tern (CAN) <i>Sterna paradisaea</i>	4	—	42.4	—	30.0	—	1.2	—	1.41	—	15.02	—	0.93	—	
Roseate Tern (MA) <i>Sterna dougallii</i>	3	—	41.6	—	30.0	—	1.0	—	1.38	—	19.70	—	0.84	—	
Sooty Tern (BHI) <i>Sterna fuscata</i>	1	—	49.4	—	34.8	—	1.9	—	1.42	—	31.35	—	1.13	—	

TABLE I. *Continued*

Species†	No. eggs‡		L(mm)		B(mm)		Wt(gm)		L/B [¶]		Vol. (cm ³)#		Thickness§	
	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH
Common (Y.-sh.) Flicker (UT) <i>Colaptes auratus</i>	6	5	27.2	27.9	21.2	21.6	0.5	0.6	1.29	1.29	6.44	6.83	0.92	0.97
Red-bellied Woodpecker (CAN) <i>Centurus carolinus</i>	4	—	26.4	—	19.3	—	0.4	—	1.36	—	5.18	—	0.86	—
Red-headed Woodpecker <i>Melanerpes erythrocephalus</i>	—	4	—	25.7	—	19.8	—	0.4	—	1.30	—	5.29	—	0.76
Hairy Woodpecker (UNK) <i>Dendrocopus villosus</i>	4	—	21.9	—	16.1	—	0.2	—	1.36	—	3.00	—	0.57	—
Downy Woodpecker (FL, AR) <i>Dendrocopus pubescens</i>	8(2)	4	18.5	19.0	14.6	15.1	0.1	0.2	1.27	1.26	2.07	2.27	0.57	0.67
Eastern Kingbird (CAN) <i>Tyrannus tyrannus</i>	4	—	24.4	—	17.2	—	0.2	—	1.41	—	3.80	—	0.57	—
Western Kingbird (CA) <i>Tyrannus verticalis</i>	5	—	24.6	—	17.6	—	0.2	—	1.39	—	4.01	—	0.56	—
Cassens's Kingbird (CA) <i>Tyrannus vociferans</i>	5	—	24.1	—	17.6	—	0.2	—	1.37	—	3.89	—	0.53	—
Scissor-t. Flycatcher (TX) <i>Muscivora forficata</i>	3	—	21.3	—	17.7	—	0.2	—	1.20	—	3.48	—	0.55	—
Great Cr. Flycatcher (UNK) <i>Myiarchus crinitus</i>	4	—	23.2	—	16.8	—	0.2	—	1.38	—	3.46	—	0.53	—
Ash-throated Flycatcher (CA) <i>Myiarchus cinerascens</i>	5	—	23.4	—	17.5	—	0.2	—	1.33	—	3.75	—	0.51	—
Eastern Phoebe <i>Sayornis phoebe</i>	—	4	—	19.0	—	14.2	—	0.1	—	1.34	—	2.01	—	0.38
Black Phoebe (CA) <i>Sayornis nigricans</i>	3	—	20.7	—	14.9	—	0.1	—	1.39	—	2.40	—	0.35	—
Say's Phoebe (KS) <i>Sayornis saya</i>	4	—	19.3	—	15.3	—	0.1	—	1.26	—	2.39	—	0.45	—
Acadian Flycatcher <i>Empidonax virens</i>	—	2	—	18.3	—	13.9	—	0.1	—	1.32	—	1.86	—	0.40
Trall's Flycatcher (UNK) <i>Empidonax traillii</i>	3	2	17.9	17.4	13.7	13.7	0.1	0.1	1.31	1.27	1.75	1.71	0.38	0.37
Least Flycatcher (MN) <i>Empidonax minimus</i>	5	—	16.0	—	12.2	—	0.1	—	1.31	—	1.25	—	0.32	—
Western Flycatcher (CA) <i>Empidonax difficilis</i>	3	—	18.8	—	13.9	—	0.1	—	1.35	—	1.91	—	0.31	—
Eastern Wood Pewee <i>Contopus virens</i>	—	4	—	18.3	—	13.6	—	0.1	—	1.34	—	1.80	—	0.38
Horned Lark (NY) <i>Eremophila arctica</i>	3	—	24.8	—	17.4	—	0.2	—	1.42	—	3.94	—	0.52	—
Tree Swallow (CA) <i>Iridoprocne bicolor</i>	3	—	17.8	—	12.9	—	0.1	—	1.38	—	1.55	—	0.38	—
Bank Swallow <i>Riparia riparia</i>	—	4	—	17.5	—	12.3	—	0.1	—	1.42	—	1.38	—	0.30
Rough-winged Swallow (PA) <i>Stelgidopteryx ruficollis</i>	3	—	17.6	—	12.8	—	0.1	—	1.37	—	1.52	—	0.37	—
Barn Swallow <i>Hirundo rustica</i>	—	4	—	21.6	—	13.7	—	0.1	—	1.58	—	2.15	—	0.35
*Cliff Swallow <i>Petrochelidon pyrrhonota</i>	—	4	—	19.4	—	13.7	—	0.1	—	1.42	—	1.91	—	0.36
Purple Martin (UNK) <i>Progne subis</i>	5	—	25.6	—	17.5	—	0.2	—	1.46	—	4.12	—	0.55	—
Blue Jay (FL) <i>Cyanocitta cristata</i>	3	4	26.5	27.5	20.5	19.8	0.4	0.3	1.29	1.39	5.82	5.70	0.70	0.64
Scrub Jay (FL) <i>Aphelocoma coerulescens</i>	3	—	26.2	—	19.6	—	0.3	—	1.34	—	5.26	—	0.60	—
Black-billed Magpie (UNK) <i>Pica pica</i>	1	—	35.5	—	23.9	—	0.6	—	1.48	—	10.62	—	0.69	—
Yellow-billed Magpie (CA) <i>Pica nuttalli</i>	3	—	31.4	—	22.4	—	0.5	—	1.40	—	8.29	—	0.71	—
Common Raven (AB, CA) <i>Corvus corax</i>	7(2)	—	46.7	—	32.5	—	1.6	—	1.44	—	25.88	—	1.08	—
White-necked Raven (TX) <i>Corvus cryptoleucus</i>	3	—	44.0	—	31.1	—	1.5	—	1.41	—	22.88	—	1.09	—

Species†	No. eggs‡		L(mm)		B(mm)		Wt(gm)		L/B"		Vol. (cm³)#		Thickness§	
	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH
Yellow-throated Vireo (NY) <i>Vireo flavifrons</i>	4	—	20.3	—	14.3	—	0.1	—	1.42	—	2.18	—	0.37	—
Red-eyed Vireo <i>Vireo olivaceus</i>	—	4	—	20.6	—	14.9	—	0.1	—	1.38	—	2.40	—	0.39
Warbling Vireo (NY) <i>Vireo gilvus</i>	4	—	19.2	—	14.3	—	0.1	—	1.34	—	2.06	—	0.39	—
Prothonotary Warbler (IL) <i>Protonotaria citrea</i>	5	—	17.6	—	14.4	—	0.1	—	1.22	—	1.90	—	0.57	—
Swainson's Warbler (GA) <i>Limnothlypis swainsonii</i>	2	—	19.7	—	14.2	—	0.1	—	1.38	—	2.12	—	0.39	—
Worm-eating Warbler (PA) <i>Helmitheros vermivorus</i>	5	—	18.1	—	14.3	—	0.1	—	1.26	—	1.94	—	0.43	—
Golden-winged Warbler (NY) <i>Vermivora chrysoptera</i>	3	—	16.8	—	13.5	—	0.1	—	1.25	—	1.61	—	0.38	—
Blue-winged Warbler (CT) <i>Vermivora pinis</i>	5	—	15.1	—	12.1	—	0.1	—	1.25	—	1.16	—	0.36	—
Yellow Warbler <i>Dendroica petechia</i>	—	4	—	16.1	—	12.6	—	0.1	—	1.28	—	1.35	—	0.38
Magnolia Warbler (NH) <i>Dendroica magnolia</i>	3	—	16.9	—	13.5	—	0.1	—	1.25	—	1.61	—	0.44	—
Black-th. Green Warbler (NY) <i>Dendroica virens</i>	3	—	19.5	—	14.3	—	0.1	—	1.36	—	2.10	—	0.38	—
Cerulean Warbler (NY) <i>Dendroica cerulea</i>	2	—	16.2	—	12.6	—	0.1	—	1.29	—	1.34	—	0.40	—
Chestnut-sided Warbler (NY) <i>Dendroica pennsylvanica</i>	4	—	16.5	—	11.8	—	0.1	—	1.40	—	1.21	—	0.35	—
Prairie Warbler (MA) <i>Dendroica discolor</i>	4	—	17.1	—	12.7	—	0.1	—	1.34	—	1.46	—	0.35	—
Ovenbird <i>Seiurus aurocapillus</i>	—	4	—	20.5	—	16.0	—	0.1	—	1.28	—	2.75	—	0.45
Louisiana Waterthrush (UNK) <i>Seiurus motacilla</i>	5	—	19.6	—	15.8	—	0.1	—	1.24	—	2.59	—	0.47	—
Kentucky Warbler (GA) <i>Oporornis formosus</i>	3	—	17.2	—	15.1	—	0.1	—	1.14	—	2.05	—	0.43	—
Yellowthroat (WV) <i>Geothlypis trichas</i>	9(2)	—	17.3	—	13.2	—	0.1	—	1.31	—	1.58	—	0.39	—
Yellow-breasted Chat (CA) <i>Icteria virens</i>	4	3	21.7	22.6	16.6	16.5	0.2	0.2	1.30	1.37	3.15	3.21	0.58	0.54
Hooded Warbler (UNK) <i>Wilsonia citrina</i>	4	—	18.3	—	14.1	—	0.1	—	1.30	—	1.92	—	0.36	—
Wilson's Warbler (CA) <i>Wilsonia pusilla</i>	2	—	15.8	—	12.5	—	0.1	—	1.26	—	1.31	—	0.33	—
American Redstart (NY) <i>Setophaga ruticilla</i>	5	—	16.1	—	12.5	—	0.1	—	1.28	—	1.31	—	0.37	—
House Sparrow (UNK) <i>Passer domesticus</i>	4	—	21.8	—	14.9	—	0.2	—	1.46	—	2.55	—	0.54	—
Bobolink (NY) <i>Dolichonyx oryzivorus</i>	5	—	23.6	—	16.4	—	0.2	—	1.43	—	3.34	—	0.47	—
Eastern Meadowlark (FL, MS) <i>Sturnella magna</i>	17(4)	5	28.1	29.5	20.9	20.0	0.3	0.3	1.34	1.47	6.46	6.19	0.60	0.59
Yellow-headed Blackbird (UT) <i>X. xanthocephalus</i>	4	—	26.2	—	17.9	—	0.2	—	1.47	—	4.38	—	0.55	—
Red-winged Blackbird (CA, FL) <i>Agelaius phoeniceus</i>	23(7)	—	23.0	—	17.0	—	0.2	—	1.35	—	3.51	—	0.52	—
Tri-colored Blackbird (CA) <i>Agelaius tricolor</i>	4	—	23.9	—	17.9	—	0.2	—	1.33	—	4.02	—	0.47	—
*Orchard Oriole <i>Icterus spurius</i>	—	4	—	19.8	—	14.1	—	0.1	—	1.40	—	2.07	—	0.35
Hooded Oriole (CA) <i>Icterus cucullatus</i>	3	—	23.7	—	15.8	—	0.2	—	1.50	—	3.12	—	0.43	—
*Northern (Baltimore) Oriole <i>Icterus galbula</i>	—	5	—	23.7	—	15.6	—	0.2	—	1.51	—	3.05	—	0.48
No. (Bullock's) Oriole (CA) <i>Icterus galbula</i>	6	—	23.6	—	16.4	—	0.2	—	1.44	—	3.34	—	0.58	—

TABLE 1. *Continued*

Species†	No. eggs‡		L(mm)		B(mm)		Wt(gm)		L/B [¶]		Vol. (cm ³)#		Thickness§	
	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH	Non-OH	OH
White-crowned Sparrow (CA) <i>Zonotrichia leucophrys</i>	4	—	22.5	—	16.3	—	0.2	—	1.38	—	3.14	—	0.55	—
Nuttall's Wh.-cr. Sparrow (CA) <i>Zonotrichia leucophrys</i>	4	—	21.6	—	16.2	—	0.2	—	1.33	—	2.97	—	0.51	—
White-throated Sparrow (NH) <i>Zonotrichia albicollis</i>	3	—	21.7	—	15.7	—	0.2	—	1.38	—	2.81	—	0.51	—
Swamp Sparrow (PA) <i>Melospiza georgiana</i>	3	—	19.3	—	14.5	—	0.1	—	1.33	—	2.12	—	0.44	—
Song Sparrow (CA, WA) <i>Melospiza melodia</i>	11(3)	4	19.2	18.8	15.1	15.0	0.1	0.1	1.27	1.25	2.30	2.21	0.53	0.52
McCown's Longspur (SD) <i>Rhyncophanes mccownii</i>	3	—	21.1	—	15.4	—	0.1	—	1.37	—	2.64	—	0.47	—

(1956) and Paganelli *et al*, (1974) was made (table 2). Differences ranged from 0.7 to 22%. Percentage differences by the Kendeigh equation were greater than the Paganelli equation in 12 of 14 species and averaged 5.7%. These differences in approximation of egg volumes could be attributed to the technique of measurement, natural variation of egg sizes within the clutch or species, biases in the formulas, or geographic differences. Paganelli *et al*, (1974) determined that technique accounted for their egg volumes to be underestimated by about 2%. Perhaps an allometric equation, based on eggshell weight might best approximate

volumes of eggshells in museum collections. Development of the formula could follow the techniques used by Paganelli *et al*, (1974). Egg volumes as obtained by external measurements were also compared to volumes obtained by water displacement in 617 Coturnix quail (*Coturnix coturnix*) eggs. Mean total egg volumes by water displacement and by the Kendeigh equation were 8.91±1.47 and 8.95±1.38, respectively, and were not significantly different from each other. The close agreement was expected since Coturnix eggs approach ellipsoids. The average elongation for 617 eggs was 1.28±0.03.

TABLE 2
Comparison of egg volumes for selected species of birds

Species	Paganelli <i>et al</i> *		Osborne and Winters		% Difference
	No. eggs	Volume* (cm ³) ± SD	No. eggs	Volume** (cm ³) ± SD	
House Wren	27	1.27± 0.13	17	1.35± 0.04	5.9
Yellow Warbler	3	1.33± 0.24	4	1.35± 0.07	1.5
Tree Swallow	5	1.71± 0.06	3	1.55± 0.18	9.3
House Sparrow	21	2.53± 0.13	4	2.55± 0.18	0.7
Brown-headed Cowbird	7	3.45± 0.44	9	3.74± 1.08	7.7
Red-winged Blackbird	18	3.46± 0.47	23	3.51± 0.29	1.4
Common Grackle	3	6.08± 0.06	8	6.14± 0.15	1.0
American Robin	6	5.88± 0.10	3	7.55± 0.22	22.0
Ring-necked Pheasant	12	30.81± 2.05	17	29.97± 4.41	2.7
European Oystercatcher	2	40.12± 2.79	2	47.91± 5.85	16.2
Double-crested Cormorant	8	45.87± 2.75	3	46.43± 1.09	1.2
Common Puffin	6	55.85± 3.44	1	60.46	7.6
Herring Gull	3	83.70± 4.91	2	102.13± 2.65	18.0
Great Black-backed Gull	9	105.11±11.43	3	115.58±16.07	9.0
Average					+5.7

*Calculated from the formula 2.48 X 10⁻² times total egg weight to the 1.118 power, after Paganelli *et al*, (1974).
**Calculated from the formula 0.524 LB², after Kendeigh *et al*, (1956).

TABLE 3
Comparison of pre-1941 egg shell thicknesses in certain raptorial and fish-eating birds

Species	Anderson and Hickey (1970b)			Osborne and Winters			% Difference
	Location*	No. eggs	Thickness Index \pm SD	Location*	No. eggs	Thickness Index \pm SD	
Common Loon	CAN	42	3.00 \pm 0.04	UNK	1	2.94 \pm —	2.0
White Pelican	West. US	102	3.26 \pm 0.03	TX	3	3.36 \pm 0.04	2.9
Brown Pelican	LA	43	2.59 \pm 0.04	LA	3	2.56 \pm 0.03	1.1
Double-crested Cormorant	Inter. NA	350	2.12 \pm 0.02	LA	3	2.19 \pm 0.02	3.2
Great Blue Heron	CAN	130	2.05 \pm 0.02	CA, NJ	10	2.12 \pm 0.02	3.3
Sharp-shinned Hawk	CAN	197	1.31 \pm 0.01	RI	3	1.48 \pm 0.03	11.5
Cooper's Hawk	CA	88	1.75 \pm 0.03	OH	7	1.73 \pm 0.04	1.1
Red-tailed Hawk	CA	187	2.25 \pm 0.01	CA	4	2.40 \pm 0.02	6.2
Red-shouldered Hawk	Great Lakes	759	1.90 \pm 0.01	MD, GA	5	1.93 \pm 0.01	1.5
Broad-winged Hawk	Inter. NA	250	1.70 \pm 0.02	OH	2	1.70 \pm 0.02	0.0
Rough-legged Hawk	Arctic NA	172	2.20 \pm 0.02	UNK	4	2.45 \pm 0.03	10.2
Golden Eagle	West. NA	290	3.03 \pm 0.02	UNK	2	2.89 \pm 0.04	4.6
Bald Eagle	FL	211	3.10 \pm 0.03	UNK	2	3.51 \pm 0.04	11.7
Marsh Hawk	Inter. NA	349	1.59 \pm 0.01	OH	4	1.43 \pm 0.02	10.1
Osprey	Eastern US	365	2.57 \pm 0.01	NJ	3	2.15 \pm 0.03	16.3
American Kestrel	Inter. NA	583	1.06 \pm 0.00	CA	4	1.05 \pm 0.01	0.9
Herring Gull	Arctic NA	94	1.80 \pm 0.02	CAN	2	1.80 \pm 0.02	0.0
Great Horned Owl	Inter. NA	134	2.01 \pm 0.03	NY	3	1.93 \pm 0.02	4.0
Common Crow	Great Lakes	105	1.00 \pm 0.03	OH	4	0.97 \pm 0.03	3.0
Average							4.9

*Abbreviations of country state, etc. follow those listed in the North American Bird Banding Manual, Vol. 1, 1976; UNK=unknown.

Shell thickness for the class (table 1) averaged 0.90 (0.20–3.51). Crane and pelican families have the thickest shells (2.82 and 2.63, respectively) followed by fulmars (2.58) and oyster-catchers (2.51). Other families with shells thicker than 2.00 include the new world vultures (2.34), loons (2.28), ospreys (2.15), and Accipitridae (2.12). Hummingbird eggs have the thinnest shells (0.20). Next in order are six families which have similar shell thicknesses, ranging from 0.34 for gnatcatchers to 0.40 for nuthatches. They include the Paridae (0.37), Tyrannid flycatchers (0.38), vireos (0.38) and new world warblers (0.39).

Anderson and Hickey (1970b) reported shell thicknesses for eggs of 25 species of raptorial and fish-eating birds. Eggs were from different localities in North America and collected prior to 1941. We compared their thickness values for 19 species common to our study (table 3). In order to reduce geographic variability we attempted to select samples from similar localities. Differences in shell thickness ranged up to 16% and

averaged about 5%. In spite of our small sample size we feel our values of thickness are quite compatible with theirs. Large differences could be due to sample size, geographic variation, or date of collection. For example, our thickness index for the Osprey (2.15) agreed more closely with their 1957 sample (2.03) from eastern US.

LITERATURE CITED

- Alsop, Frederick J. III. 1972. Eggshell thickness from Red-winged Blackbird (*Agelaius phoeniceus*) populations with different exposure to DDT. Unpubl. Ph.D. thesis, University of Tennessee, Knoxville.
- American Ornithologists' Union. 1957. Checklist of North American birds. Fifth Ed. Lord Baltimore Press, Inc., Baltimore, Md. 691 p.
- Anderson, D. W. and J. J. Hickey. 1970a. Oölogical data on egg and breeding characteristics of Brown Pelicans. *Wilson Bull.* 82: 14–28.
- . 1970b. Eggshell changes in certain North American birds. *Proceed. 15th Intern. Ornith. Cong., Hague.* 514–540.
- , H. G. Lumsden, and J. J. Hickey. 1970. Geographic variation in the eggshells of Common Loons. *Canadian Field-Naturalist* 84: 351–356.

- Ar, A., C. V. Paganelli, R. B. Reeves, D. G. Greene, and H. Rahn. 1974. The avian egg. Water vapor conductance, shell thickness, and functional pore area. *Condor* 76: 153-158.
- Asmundson, V. S., G. A. Baker, and J. T. Emlen. 1943. Certain relations between the parts of birds' eggs. *Auk* 60: 34-44.
- Banks, R. C., M. H. Clench, and J. C. Barlow. 1973. Bird collections in the United States and Canada. *Auk* 90: 136-170.
- Barth, E. K. 1968. Egg dimensions and laying dates of *Larus marinus*, *L. argentatus*, *L. fuscus* and *L. canus*. *Nytt Mag. Zool.* 15: 5-34.
- Bent, A. C. 1919 onwards. Life histories of North American birds. U.S. Natl. Mus., Bull. no. 107, *seq.*
- Burger, J. 1973. Egg size and shell thickness in the Franklin's Gull. *Auk* 90: 423-426.
- Clench, M. H., R. C. Banks, and J. C. Barlow. 1976. Bird collections in the United States and Canada: addenda and corrigenda. *Auk* 93: 126-129.
- Coulson, J. C., G. R. Potts, and Jean Horobin. 1969. Variation in the eggs of the Shag (*Phalacrocorax aristotelis*). *Auk* 86: 232-245.
- French, R. 1973. A guide to the birds of Trinidad and Tobago. Livingston Publ. Co., Wynnewood, PA. 470 p.
- Gemperle, M. E. and F. W. Preston. 1955. Variation of shape in the eggs of the Common Tern in the clutch sequence. *Auk* 72: 184-198.
- Grossfeld, J. 1938. Handbuch der Eierkunde. Julius Springer, Berlin. 375 p.
- Hefner, R. A. 1974. The zoology Museum of Miami University Vol. II. Miami University, Oxford, Ohio. 42 p.
- Hickey, J. J. and D. W. Anderson. 1968. Chlorinated hydrocarbons and eggshell changes in raptorial and fish-eating birds. *Science* 162: 271-273.
- Jefferies, D. J. 1969. Induction of apparent hyperthyroidism in birds fed DDT. *Nature* 222: 578-579.
- Kendeigh, S. C., T. C. Kramer, and F. Hammerstrom. 1956. Variations in egg characteristics of the House Wren. *Auk* 73: 42-65.
- Klaas, E. E., H. M. Ohlendorf, and R. G. Heath. 1974. Avian eggshell thickness: variability and sampling. *Wilson Bull.* 86: 156-164.
- Nelson, J. B. 1966. The breeding biology of the Gannet (*Sula bassana*) on the Bass Rock, Scotland. *Ibis* 108: 584-626.
- Olsson, J. 1936. Proc. World's Poultry Congr. (Leipzig) 6: 310-320.
- Paganelli, C. V., A. Olszowska, and A. Ar. 1974. The avian egg: Surface area, volume and density. *Condor* 76: 319-325.
- Palmer, R. S. 1962. Editor, Handbook of North American birds. Vol. 1. Yale University Press, New Haven.
- Porter, R. D. and S. N. Wiemeyer. 1969. Dieldrin and DDT: Effects on Sparrow Hawk eggshells and reproduction. *Science* 165: 199-200.
- Preston, F. W. 1953. The shapes of birds' eggs. *Auk* 70: 160-182.
- . 1957. Two new devices for measuring the shapes of birds' eggs. *Auk* 74: 386-388.
- . 1968. The shapes of birds' eggs: Mathematical aspects. *Auk* 85: 454-463.
- . 1969. Shapes of birds' eggs: Extant North Americans families. *Auk* 86: 246-264.
- . 1974. The volume of an egg. *Auk* 91: 132-138.
- Ratcliffe, D. A. 1967. Decrease in eggshell weight in certain birds of prey. *Nature* 215: 208-210.
- . 1970. Changes attributable to pesticides in egg breakage frequency and eggshell thickness in some British birds. *J. Appl. Ecol.* 7: 67-113.
- Richdale, L. E. 1955. Influences of age on size of eggs in Yellow-eyed Penguins. *Ibis* 97: 266-275.
- Romanoff, A. L. and A. J. Romanoff. 1949. The avian egg. Wiley and Sons, NY. 918 p. ear dimensions. *Emu* 65: 227-288.
- Schönwetter, M. 1960-1972. In W. Meise (ed.) Handbuch der Oologie, Lief. 1-19. Akademie Verlag, Berlin.
- Shott, A. R. and F. W. Preston. 1975. The surface area of an egg. *Auk* 77: 103-104.
- Smith, H. G., R. K. Burnard, E. E. Good, and J. M. Keener. 1973. Rare and endangered vertebrates of Ohio. *Ohio J. Sci.* 73: 257-271.
- Stonehouse, B. 1966. Egg volumes from linear dimensions. *Emu* 65: 227-288.
- Tatum, J. B. 1975. Egg volume. *Auk* 92: 576-580.
- Wallace, G. J., P. L. Ames, W. E. Banko, J. R. Jehl, D. B. Peakall, S. R. Wilbur, L. E. Williams, Jr. 1972. Report of the Committee on Conservation, 1971-72. *Auk* 89: 872-878.
- Worth, C. B. 1940. Egg volumes and incubation periods. *Auk* 57: 44-60.